POLLINATION SYSTEMS IN NAMAQUALAND: A RESPONSE TO A PREDICTABLE WINTER RAINFALL REGIME

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M. G. Raine
Student No.:RNXMIC003

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I don't know this literature ...

Essay finishing stopping – not defining concepts
too wide

No data presented
Unethical transfer of ideas
How much was longer after Friday?

682.

Introduction

Located in north-western South Africa there exists a desert environment unlike any other in the world - the succulent karoo. This region is unusual in that it is dominated by leaf-succulent shrubs(Milton et al, 1997; Cowling et al, 1998). In addition, the succulent karoo has remarkably high levels of both diversity (>5000 species in 100251 km^2) and the degree of endemism (>50%) of species (Milton et al, 1997). Within this biome is a strongly winter-rainfall region formally recognised as the Namaqualand-Namib Domain of the succulent karoo floristic region (Cowling et al, 1998). Alpha diversity in Namaqualand, is very high - with a mean of 74 species having been recorded at the 0.1 ha scale - resulting in the existence of many co-occurring species at any locality (Cowling et al, 1998). Regional diversity in Namaqualand, is extraordinarily high for an arid land, supporting more species per unit area than other equivalent arid regions in the world. It is therefore a somewhat unique system with a number of extremely interesting features.

Namaqualand is characterised by a number of unique plant ecological features which are mediated by a unique selective regime - highly predictable annual rainfall and a moderate temperature regime throughout the year (Cowling et al, 1998;Struck 1994a). According to Cowling et al (1998), the regional richness of Namaqualand is explained best by a measure of environmental heterogeneity (length of the rainfall gradient) and favourableness (rainfall reliability). Consequently, the species rich regions in the Karoo-Namib correspond with long moisture gradients and predictable seasonal rainfall.

It is posited that these rainfall and temperature regimes are also responsible for the brief, but copious flower display during spring time, a renowned feature of the arid region commonly known as Namaqualand (Struck, 1994a and b). The remarkable feature of this flowering episode is that there is a notable synchronisation of flowering, where a great variety of mass-flowering shrubs, and a rich flora of therophytes and geophytes may virtually cover the landscape with carpets of blooms after ample rains. At this stage it in important to define the term "mass-flowering" - a term synonymous with the blooming period in the Namaqualand region. Mass-flowering in the context of this essay refers to the multi-species synchronised flowering event in spring, during which time 90% of the shrubby perennial species and virtually all of the annuals flower. The term may also describe the phenomenon of say, one species producing an extremely

large number of flowers at any one time. This essay shall discuss the vigour of blooming in response to environmental cues, however the major viewpoint being expressed adopts the former definition of mass flowering. In particular, this essay details the response of the pollination syndromes to this feature of synchronised flowering.

The anthophilous insects perspective of these flowering events must be one of sheer delight - as deduced from the number of blooms available as potential food sources in the form of nectar and/or pollen - or one of great confusion. Which flower should an insect visit if it is to maximise its success of foraging activity and minimise its energetic expenditure? What patterns exist, if any, in the floral morphology of the flowering species which determine plant-pollinator associations? Is the flower architecture of all the flowers similar, such that an insect can forage locally on any flowering species, or does there exist some differentiation in floral morphology between species which promote pollinator associations? Such questions are fundamental in the analysis of pollination syndromes in an environment which seems to promote the synchronisation of flowering and hence, pollinator competition.

From a plants perspective there are a number of considerations influencing pollinator associations. The seasonality of flowering is largely determined by availability of moisture to meet the physiological demands of producing blooms (Struck, 1994a). The amount of energy allocated to producing flowers, energetically expensive in terms of pollen and nectar production, appears paradoxical for an arid region which receives a winter rainfall of less than 150mm per annum (Cowling et al, 1998). It is posited that the high winter rainfall reliability of Namaqualand is the primary explanation of the biologically unusual patterns and processes of the region (Cowling et al, 1998).

The flowers are therefore faced with a significant problem - flowering must track the relatively high available moisture supported by the predictable winter rains, resulting in a relatively short period in which blooming is energetically favourable. Consequently, a vast majority of the co-occurring species flower from late winter to early spring, and therefore all compete for pollinators. Producing one flower in amongst thousands, the chances of being pollinated should be very small, unless there exists some adaptation which makes it more attractive to potential pollinators. It is these adaptations in which we are interested.

Cues for Flowering and Insect Emergence

Flowering is greatly moulded by the prevailing weather conditions (struck, 1994a; Cowling et al, 1998; Milton et al, 1997). The relative predictability of rainfall between years, in conjunction with the relatively mild winter growing season temperatures have resulted in a winter growth phenology. Autumn rains induce vegetative development in both perennial and annual species, actively growing to reproductive maturity during the winter months (Manning and Goldblatt, 1996). The vigour and to some extent the duration of flowering is subject to the amount of precipitation received before and during the blooming season. The result of high or low moisture availability is most easily seen in the flowering performance of the annual flora. A season of high rainfall, relative to the mean annual rainfall of the region, results in the production of a greater number of flowers, creating those spectacular displays which are driving the tourist industry.

However, rainfall is not the overriding environmental factor controlling the timing of flowering (Struck, 1995). The onset of the blooming season varies from year to year, however, the sequence of flowering phenologies of the co-occurring species remains largely unchanged. This is because the timing of the blooming - as part of the yearly cycle of seasonal activity and dormancy - is linked to the more predictable triggers mediated through temperature changes. The timing of flowering is indirectly linked to the first considerable drop in air temperatures in autumn and/or by the increase in temperatures in the beginning of spring.

In contrast, species composition and the number of individuals of therophytes and geophytes in flower is largely determined by the pattern and amount of seasonal precipitation (Struck, 1995). Fluctuations in the seasonal rainfall, although predictable in terms of its occurrence from one flowering season to the next, may promote a species blooming in one year and retard it in another. The consequences of this variation in the composition of flowering plants in a given locality, in response to variations in precipitation, has important influences on pollination syndromes in Namaqualand. These shall be discussed in further detail.

Flowering responses are also related to morphological and physiological constraints imposed on species. For example, non-succulent shrubs produced the greatest number of flowers in moister years, whereas succulents flowered most prolifically in a dry year (Struck, 1994b).

Thus, we have determined that although unpredictable in terms of species responses to variations in precipitation, flowering occurs in a more or less fixed sequence at a given locality. This allows the anthophilous insects to emerge from diapause accordingly, allowing the insect fauna to track the availability of their food source. The co-ordination in timing of flowering and insect activity is possible, since both are ultimately triggered by the same cues - changes in temperature and moisture availability (Struck, 1994b). Thus, although the blooming period is short, in response to available moisture, plants potentially have a reliable means of ensuring pollination. The Namaqualand flora is dominated by short-lived species which utilise shallow root systems to effectively compete for water uptake (Cowling et al, 1998). These shallow root systems provide little buffering against periods of low rainfall, making Namaqualand plants sensitive to drought stress. Consequently, these short-lived species rely on continuous seedling establishment for persistence, making plant reproductive processes very important. Thus, reliable co-ordination between flowering and insect activity is essential in an environment such as Namaqualand.

Anthophilous Insect Fauna

Abundance of Insects

The obvious question one should ask next, is wether the abundance of the anthophilous insect fauna parallels the abundance of flowering species. One would predict that the large number of blooms would be complimented by an equally impressive emergence of the insect fauna. In addition, the predictability of a potential food supply should provide a strong positive selection for the predictable emergence of a large number of pollinators. But despite the rich supply of floral reward - as deduced from the number of flowers offered to insects during the flowering season - the abundance of anthophilous insects is relatively low (Struck, 1994b).

Surely these two may not be connected?

Environmental Constraints

The anthophilous insects enter diapause during the stressful months of summer and autumn, when available moisture levels are extremely low. In addition, the insects are food-limited as very few plant species flower outside the main spring flowering period. Furthermore, weather conditions frequently interfere with insect activities. Fog or cloudy weather with low temperatures and rain occur particularly during the spring flowering season, which is also the principle flight period of the anthophilous insects. Strong winds are common throughout the year and reduce the times of insect activity even further (Struck, 1994b).

Diversity

In terms of diversity, bees, masarine wasps and bee-flies appear to be the most important pollinators (Struck, 1994 a and b). These three groups depend on nectar as a direct energy source for adult flight. In addition, bees and masarine wasps collect pollen for larval provision, while female bee-flies frequently ingest pollen as a protein source for egg maturation. This high degree of dependence on a floral diet makes all three groups highly motivated flower visitors.

There appears therefore to be a disjunction between the abundance of potential food sources and the corresponding number of anthophilous insects which are associated with them. Advertising is an expensive exercise for the plant, particularly in arid environments. Much energy is invested in nectar and extra pollen, which serve as rewards for the attracted insects. This additional cost would be completely wasted if flowering plants did not ensure that the insects were effective at pollination and not merely benefiting from the rewards. Furthermore, the degree of diversification shown by the flora of the region appears not to be parallelled by the anthophilous insect fauna.

From these disjunctions between plants and their pollinators emerge two important questions. Firstly, how does this rather paradoxical ratio of flowering plant species : pollinators influence pollen limitation, and an associated failure of fruiting? Secondly, how has this mismatch influenced plant-pollinator associations?

Pollen Limitation

The pollination ecology of this region has been seriously neglected. Although conditions optimal for pollinator activity during the flowering season are not particularly common, there is as yet no research to test for pollinator limitation in Namaqualand (Cowling et al, 1998). In a recent study carried out by Johnson and Bond (1997), they examined the implications of pollen limitation on the fruiting success in Cape wildflowers, brought about by the low numbers of insects in the fynbos biome. Pollen limitation was inferred from the levels of stigmatic pollen deposition, and fruit production in populations of orchids.

Evidence of pollen limitation

Pollen was deposited on only a small percentage of stigmas (median= 34%) in 41 orchid populations. Natural levels of fruit set per plant among the 12 study populations varied from 4% to 64% (median=32%). Limited pollen availability appears to account for these low levels of fruit set, as supplementary hand pollination increased fruit set significantly in 11 out of the 12 study populations. The hand pollinated treatments had a fruit set varying from 24% to 96% (median=70%), with fruit set being increased by more than 100% by hand pollination in approximately half of the study populations.

Possible Causes of pollen limitation

The most plausible explanations for the low pollination success of the orchid study populations, are a general scarcity of pollinators in the fynbos region; lack of floral rewards in the flowers; and the effects fire has on depleting pollinator populations (Johnson and Bond, 1997).

are you extrapolating from
orchids → fynbos → Namaqualand without
even guessing + just doing it?

Implications of Pollen Limitation

Pollen limited plants should undergo selection for floral traits which enhance pollen receipt (Johnson and Bond, 1997). The evolution of floral characters brought about by the influence of pollen availability, is dependant on the degree to which pollen limits plant lifetime fitness. It is posited that an increase in fruit production would lead to increased lifetime fitness. Consequently, the *Orchidaceae* show extensive radiation in floral morphology - including traits which enhance pollen receipt and hence, fruit production- and a wide diversity of specialised pollination systems. These plant-pollinator associations are aimed at increasing pollination success, and consequently plant lifetime fitness by increasing fruit set. Stebbins (1970) argued that floral radiation was induced by pollen limitation, arguing that "plants which colonise regions in which their pollinators are scarce, may either evolve flowers which are more attractive to the same pollinator, or may shift to other more effective pollinators".

Namaqualand is characterised by a low abundance of anthophilous insects, and a large number of flowers in need of pollination. Although there is as yet no research to test for pollinator limitation (Cowling et al, 1998), we can infer from the disproportionate ratio of flowers to pollinators, that pollen limitation may in fact be a reality in Namaqualand. What features of floral morphology, if any, reflect Stebbin's hypothesis of floral radiation and specialised pollination systems in response to pollen limitation in Namaqualand?

Pollination Syndromes in Namaqualand

A number of specialised pollination syndromes exist in Namaqualand, indicating that floral characteristics are under strong pollinator-specific selection (Cowling et al, 1998).

Pollination Guilds

A guild of 28 winter and spring flowering species of two plant families, *Iridaceae* and *Geraniaceae*, from six genera is pollinated exclusively by two long-tongued flies of the family *Nemestrinidae* (Manning and Goldblatt, 1996). Plants pollinated by these two flies share a suite of convergent floral characteristics, including a straight or slightly curved floral tube 20mm-70mm long. In addition they have short petals coloured predominantly dark blue or crimson with

pale nectar guides, and anthers and stigmas exerted from the floral tube. The length of the floral tube prevents insects, including a variety of bees, wasps and other flies that pollinate plants which co-occur with members of the long-tubed flower guild, from obtaining nectar (Goldblatt and Manning, 1996). Members of this guild are therefore exclusively pollinated by these two long-tongued flies.

Within the collective range of the plant members of the guild, the ranges of two or more individual species usually overlap, but no more than four guild members co-occur locally. The combined ranges of both long-tongued fly species fall entirely within the main range of the plant species, according exactly with the area within which two or more plant species occur (Manning and Goldblatt, 1996). In Namaqualand, *Lapeirousia*, *Pelargonium* and *Babiana* co-occur locally and are visited indiscriminately by *Prosoeca peringueyi*. There is therefore the potential for pollen contamination, as the long-tongued fly carries pollen on its body from all three species.

Members of this guild force their pollinators to make maximum contact with the anthers and stigmatic surfaces, as they block the entrance to the floral tube. In addition, having a tube length longer than the tongues forces the flies to reach right into the opening of the floral tube in order to reach the nectaries at the bottom of the floral tube, thereby ensuring maximum contact with the reproductive surfaces. Pollen contamination of one species by that of another is minimised or prevented by the use of different pollen deposition sites. The pollen of each of the co-occurring plant species is placed on different parts of the insects body, which corresponds to the positioning of the anthers and stigmatic surfaces of the respective plants.

Due to the mechanical constraints on flower architecture, and the limited number of deposition sites on the insects body – four mutually exclusive sites have been identified – there is a limit to the number of species that can enter the guild at any locality (Manning and Goldbaltt, 1996). Thus, pollen contamination is a significant factor influencing species packing, resulting in the niche offered by pollination by *P. peringueyi* becoming saturated by the presence of more than three co-flowering species. The presence of four similarly adapted species in a given locality is rare.

This *P. peringueyi* pollination guild involving the long-tongued flies and their tubular flowers, provides evidence of selection for traits which enhance pollen receipt in a number of flowering plant species. This shift to a more effective pollinator is parallelled by the evolution of floral characters, which by enhancing the plants pollination success should result in an increase in the plants lifetime fitness. Thereby supporting Stebbin's hypothesis of floral radiation brought about by a scarcity of pollinators.

Specific plant-pollinator associations

A further example of specific plant-pollinator relationships in the Namaqualand region is that of the annual, *Gorteria diffusa* and the small bee-fly, *Megapalpus nitidus*. *Gorteria* has a number of raised black spots on the ray florets, which are strikingly similar in both size and colouration to the actual *M. nitidus* individuals. It is argued that these raised structures mimic the pollinating flies which aggregate in flowers (Johnson and Midgley, 1997).

In order to identify the function of these black spots, Johnson and Midgley (1997) performed a number of manipulation experiments on the capitula of *Gorteria*. The removal of spotted ray florets from the capitula of *Gorteria* resulted in a highly significant decrease in the number of visits received by *M. nitidus*, relative to control capitula, that had an equivalent number of plain ray florets removed. A further experiment which involved the replacement of natural spots with similar-sized black ink spots, also resulted in a very significant decrease in the number of visits. This suggests that not only are the flies responsive to the presence of the raised black insect-like structures, they are also responsive to details in the structure and reflectance patterns of the natural spots.

The intricate nature of this attraction lies in the morphology of the ray florets. SEM micrographs reveal that the spots comprise a number of different epidermal cell types. The central reflective white spot consists of smooth walled cells, and is surrounded by large papillate masses of cells which are responsible for its raised warty appearance.

Ultra-violet photographs reveal that while most of the dark region of the spot are UV absorbent, the centre and outer periphery of each spot are UV reflective. This central reflective spot is similar in appearance to the highlight on the thorax of the flies. In addition, the tips of the papillate masses surrounding the centre of each spot are also UV reflective, resulting in a sparkling appearance in sunlight strikingly similar to the dorsal surface of the flies.

Copulations commonly occur on the capitula of *Gorteria*, where the flies land directly on other flies sitting on the capitulum. This behaviour is remarkably similar to the response shown by flies towards the raised black spots on the capitulum, indicating an attraction to these mimics. These mate-seeking responses account for male flies landing repeatedly on the spots, while simple aggregation responses may attract both male and females to *Gorteria*. A reward in the form of both pollen and nectar then entices the flies towards the disc florets where they forage, and thereby facilitate pollination.

However, specific plant-pollinator syndromes are not common in Namaqualand, with only 30% of the species having these specific associations. The remaining 70% of the species have opted rather paradoxically to blend together and have a convergent floral design – a large, open, brightly coloured, typically actinomorphic flower (Struck, 1994b). Most of the endemic Namaqualand pollinators are generalists, which pollinate the predominant large, open flowers characteristic of the *Mesembryanthemaceae* and *Asteraceae* (Cowling et al, 1998).

Convergence of Floral Design

I have mentioned that a consistent flowering sequence occurs in Namaqualand. Since insects use the same environmental cues which trigger flower emergence, there is potential to synchronise the flowering of the host plant with the foraging activities of the insects. This synchronisation has the potential to facilitate the formation of plant-pollinator specialisations (Struck, 1994b). In addition, the short blooming period characteristic of this arid region should promote specialisations. Due to the limited time frame in which foraging activities occur, competition is likely to be reduced if anthophilous insects specialise on different host plants.

So why does the pollination ecology of Namaqualand seem to favour generalists? According to Struck (1994b), the prevalence of specialists in arid areas is unlikely, provided that specialisation occurs at the expense of the ability to utilise alternative host plants.

Variations in climatic conditions influences both the timing of flowering and the composition and diversity of flowering therophytes and geophytes in the blooming season. Furthermore, variations in precipitation may result in the promotion in the vigour of a species blooming in one year, and the retardation in another. The patchy structure of the vegetation also contributes to the variations in the composition of the flowering community at a given locality, resulting in a variable spatial distribution of floral resources.

The variation in flowering in the plant community is parallelled by variations in the yearly composition and abundance of insects in response to climatic variations (Struck, 1994b). Consequently, this results in variation in their flower visitation behaviour and hence, in variations in the frequency and distance of pollen flow for the host plants. The host plant therefore experiences a "spatio-temporal mosaic of pollinators". This results in inconsistent selective pressures preventing further specialisations to a particular group of pollinators. Thus, from the insects perspective these variations of floral resources between blooming periods may favour an opportunistic use of a broad range of host plants.

However, having a generalist pollinator which randomly visits species with these convergent floral designs, has the potential to result in pollen contamination. Mesembs adopt the general open flower typical of generalist pollination syndromes. Namaqualand comprises an extremely high diversity of mesembs, each species producing its own brightly coloured glossy flower, making them candidates for pollen contamination (Hartmann, 1991). Perennial succulents such as mesembs face one problem which annuals do not - they cannot rely on an abundance of anthophilous insects throughout the year. Despite the fact that being perennial they have the option of flowering at any time of the year, most flower in spring and thus join the competition for pollinators.

Mesembs have solved this problem to a certain extent by evolving several flower designs which differ subtly in the arrangement of the stamens, stigmas and petals (Hartmann, 1991). Each arrangement allows only insects of a certain size and shape to reach into the flower. Arrangements of reproductive surfaces also determine placement of pollen deposition on the insects body, thereby promoting cross pollination. Thus, although mesembs are subject to the effects of climatic variation on their flowering phenologies, and have adopted a generalist-pollinated floral morphology, they are promoting pollinator fidelity by subtle arrangements of floral morphology. An example of such an association is that of the solitary wasps of the family *Masaridae*, which show a clear preference for foraging on mesemb flowers (Gess and Gess, 1989 and 1990). Most have unusually long tongues, which in a similar way to the long-tongued fly pollination guild, enables them to tap hard-to-reach nectaries that co-occurring anthophilous insects with short tongues, cannot.

Conclusions

Thus an overview of the pollination syndromes and associated radiation in floral morphology, provides some evidence which supports Stebbin's hypothesis of pollen limitation. The low abundance and relatively low diversity of anthophilous insects in Namaqualand appears to have resulted in the extensive radiation in floral characters. The paucity of empirical data supporting the notion of pollen limitation, necessitates further research in the pollination ecology of the region. In particular, research should concentrate on finding evidence for a reduction in fruit set resulting from pollen limitation. By furthering our knowledge in this aspect of the ecological functioning of Namaqualand, we might be able to better understand and explain the observed pollination syndromes.

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